

# Pseudo-operculate Pulmonate Land Snails from New Caledonia

by

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*Abstract.* Two genera of New Caledonian land snails, *Pararhytida* Ancey, 1882 and *Rhytidopsis* Ancey, 1882, have a thick oval mass of densely compacted connective tissue formed on the dorsal side of their tail. This functions as an operculum to block the shell aperture when the animal retracts, and is named the pseudo-operculum. They are the only pulmonate land snails to have evolved a functional equivalent of the prosobranch operculum. *Pararhytida* inhabits dense leaf litter on the ground, while *Rhytidopsis* is an arboreal genus. Shells of both genera are very large compared with other charopid genera. The pseudo-operculum may have evolved under predation pressure from the large New Caledonian carnivorous land snails belonging to the genera *Ouagapia* Crosse, 1894 and *Ptychorhytida* Möllendorff, 1903 (family Rhytididae), and may have an exaptive value for size increase in leaf litter and for colonizing arboreal habitats in New Caledonian rain forests.

## INTRODUCTION

THE PRESENCE of a horny or calcareous disk on the dorsal surface of the tail is one of the most obvious characters separating the prosobranch gastropods from the pulmonates. Among the latter, larval stages of the marine Onchidiidae (FRETTER, 1943), Otinidae, Ellobiidae, and Amphibolidae (HUBENDICK, 1978) retain the operculum, but it persists in adults of only two genera of Amphibolidae, *Salinator* Hedley, 1900 and *Amphibola* Schumacher, 1817. No land or fresh-water pulmonates have an operculum.

The fresh-water and terrestrial prosobranchs use the operculum both as a means of retarding water loss and as defense against predators. The effectiveness of the oper-

culum as a seal in excluding environmental dangers is shown by the example of the fresh-water prosobranch *Pomacea cumingii* (King & Broderip, 1831) from Panama, whose relatively thin and horny operculum permitted survival through a more than one hour immersion in a standard alcohol-formalin amphibian killing solution (NETTING, 1936). Many terrestrial prosobranch genera independently have evolved accessory breathing tubes in the shell itself to permit gas exchange during diapause (REES, 1964:58-65, pls. 3-5), as their calcareous opercula provide extremely tight-fitting seals.

In most terrestrial pulmonates, defense against predators and retardation of water loss are functionally separated. Pulmonates secrete a sheet of mucus across the ap-

erture which may retard water loss during diapause. This sheet may or may not be heavily calcified, and may be with or without a special breathing pore. Various structural and behavioral characteristics are used in defense against predation. Among the structural modifications may be development of a thick shell to defeat gnawing, provision of internal apertural barriers to prevent ingress by small arthropods (SOLEM, 1972), or sealing of the shell to a rock or piece of wood with mucoid cement so that removal requires considerable force. Nearly all members of the family Clausiliidae make use of a special structure, the clausilium, in addition to large apertural barriers, to close the aperture. Evolution of this structure from a columellar barrier that became detached has been postulated by NORDSIECK (1982). Shell color patterns may be effective in confusing potential predators (CAIN, in press). Behavioral adaptations include habitat shifts such as nightly tree climbing to avoid a nocturnal ground foraging predator, or day-time retreat into narrow crevices to avoid a diurnal predator. A few pulmonate species are known to secrete mucus-containing irritating chemicals, for example *Liguus* (EISNER & WILSON, 1970). The endemic ant *Camptonotus* was found to be repelled by *Liguus* mucus, but the introduced fire ant *Solenopsis geminata* (Fabricius) is successful in feeding on *Liguus* (TUSKES, 1981). Other species, such as *Sultana sultana* (Dillwyn, 1817), have a very sticky mucus that will engulf small predators (TILLIER, 1980:71). Veronicellid slugs in Samoa are a major problem to chicken owners, as their mucus can kill the fowls (SOLEM, 1971).

Only one other land pulmonate has been reported previously to have a mechanical device for shell closure, the enigmatic *Thyrophorella thomensis* Greeff, 1882 from Sao Thomé. This species is described as having a loose flap of the shell, connected only to the upper palatal margin of the shell lip, that can fall down over the aperture and then later be pushed up by the extending snail (GREEFF, 1882, 1884; GIRARD, 1893, 1895). The flap itself is not attached to the snail's body, and thus is not homologous to the operculum, nor can it function as a tight seal. Only fragmentary data have been published on the anatomy of *Thyrophorella* (above references), and whether it actually should be a monotypic family, as customarily listed, is uncertain. We have been unable to find later references to collections of this species, and the materials taken by Newton and reported on by GIRARD (1893, 1895) probably were destroyed in the fire at the Museu Boçage in Lisbon several years ago. Pending collection of new material and detailed anatomical study, this species will remain a puzzle.

The discovery that two genera of New Caledonian pulmonate land snails have a "pseudo-operculum" developed on the dorsal side of their tail is of general interest. When the snail is retracted into the aperture (Figure 1), this structure effectively blocks the opening and thus functions in an analogous way to a prosobranch operculum.

#### OCCURRENCE OF THE PSEUDO-OPERCULUM

The described land snail fauna of New Caledonia numbers only about 110 species (FRANC, 1957; SOLEM, 1961), but recent collections by P. Bouchet, P. Mordan, L. Price, A. Solem, A. Tillier, S. Tillier, and assistants indicate an actual diversity level of 300–400 species (Tillier, in TILLIER & CLARKE, 1983). The dominant group in terms of species numbers is the Charopidae (*sensu* SOLEM, 1983; listed as Endodontidae by FRANC, 1957, and SOLEM, 1961). More than half of the described New Caledonian land snail species belong to the Charopidae. New discoveries probably will increase this proportion.

Two charopid genera, *Rhytidopsis* Ancey, 1882 and *Pararhytida* Ancey, 1882, currently being revised (Tillier & Mordan, in preparation), share development of the pseudo-operculum and unique structures in the terminal female genitalia. Preserved specimens are available now for most other New Caledonian charopids, but no trace of a pseudo-operculum has been seen by the authors in any other taxa. Once seen and recognized, it will not be forgotten, although two malacologists who reported on the anatomy of *Pararhytida dictyodes* (Pfeiffer, 1847) surprisingly did not mention it (FISCHER, 1875; STARMÜHLNER, 1970:302–305).

*Rhytidopsis chelonites* (Crosse, 1868) is the only described species correctly assigned to *Rhytidopsis* (Tillier, unpublished results). *Rhytidopsis* ranges from Mt. Humboldt, somewhat north of Nouméa, to the southern tip of New Caledonia. In recent years, living specimens have been collected in rain forests at 150 to 1350 meters elevation, always from tree trunks or from the underside of leaves. The shell is relatively small (diameter 6–8 mm), flammulated to dotted in color pattern, and without major sculpture; the umbilicus is minute, and the shell slightly carinated at the periphery. Other taxa traditionally assigned to *Rhytidopsis* on the basis of general conchological similarity (see FRANC, 1957; SOLEM, 1961) also are arboreal, but have very narrow and elongated tails with a prominent caudal horn, often strongly sculptured shells, and no trace of a pseudo-operculum. Eventually they will be transferred into other genera.

*Pararhytida*, as revised by Tillier & Mordan (in preparation), excludes the taxa *Micromphalia* Ancey, 1882 and *Plesiopsis* Ancey, 1888. It includes six species, several of them new. *Pararhytida* ranges throughout the main island of New Caledonia and the Belep Islands, but is absent from the younger Loyalty Islands. Old records from the Isle of Pines have not been confirmed in recent decades. *Pararhytida* is found in most forest patches, excluding the high altitude rain forests and the very dry lowland forests. The largest species, *Pararhytida dictyodes* (Pfeiffer, 1847), ranges over the entire island and is quite variable. It is possible that it includes a complex of cryptic species. The remaining taxa show restricted ranges that correlate with



Figure 1

Retracted specimen of *Pararhytida dictyodes* showing functional position of the pseudo-operculum (Photograph by A. Solem).

particular rainfall regimes (Tillier & Mordan, in preparation). All species of *Pararhytida* are litter dwellers, and they are especially common inside the sheath portions of fallen palm fronds. They have not been taken under logs or in the rotting wood habitats utilized by other New Caledonian charopids. In most species the shell is sharply carinated and the umbilicus is wide. Adult shell diameter within *Pararhytida* is from 14 to almost 37 mm.

Thus, *Rhytidopsis* and *Pararhytida* differ in shell shape, size, ecology, and geographic range. Their monophyly is suggested by their unique pseudo-opercula and structures in the terminal genitalia.

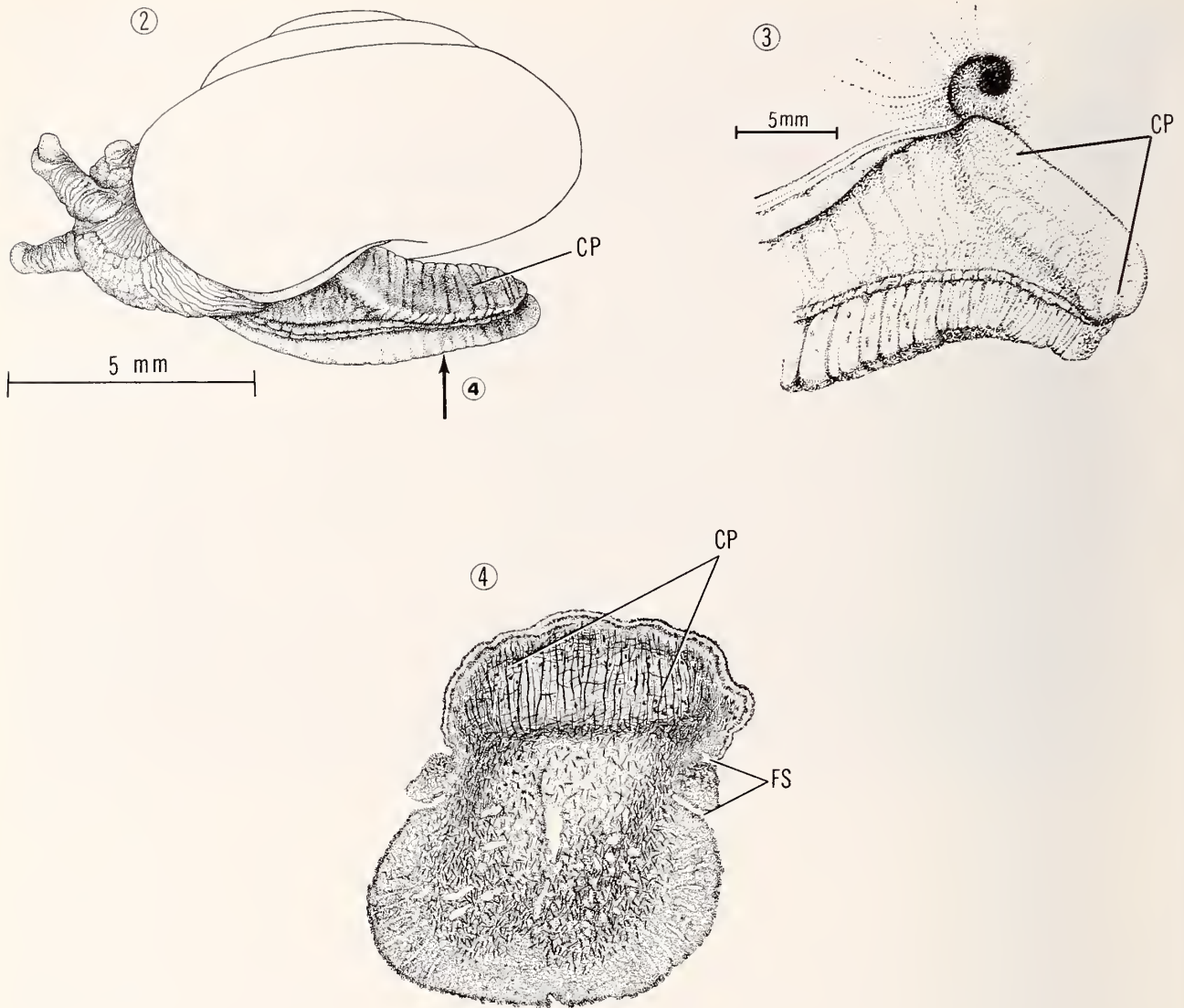
#### STRUCTURE AND FUNCTIONING OF THE PSEUDO-OPERCULUM

In both *Rhytidopsis* (Figure 2) and *Pararhytida* (Figure 3) the tail is relatively short and broad. The dorsal portion is clearly flattened and expanded into an elongately oval disk that extends from the visceral stalk to the tip of the tail. Its posterior margin can be rounded or narrowly tri-

angular, and varies individually. This novel structure is here named the pseudo-operculum.

The pseudo-opercula of two species of *Pararhytida*, *P. dictyodes* and *P. mouensis* (Crosse, 1868), have been examined histologically in longitudinal and transverse section, and are essentially similar in structure. The pseudo-operculum is composed of a thick pad of irregularly interwoven fibers underlying a single layer of epidermis. Staining with Masson's trichrome shows these fibers to be composed of collagen. The pad extends from just above the supra-pedal grooves to the top of the tail. It is extremely difficult to cut and almost impossible to tear. While the covering epithelium can be ruptured very easily, and was lost from much of the histological material studied here, the fibrous layer resists disturbance.

In section the pseudo-operculum may be broadly divided into two regions, which appear more sharply differentiated in *Pararhytida mouensis* than in *P. dictyodes*. Immediately below the epidermis lies a dense mass of collagen fibers with only a very few weak muscles. Beneath this is a rather more deeply staining layer of collagen, containing



#### Explanation of Figures 2 to 4

Figure 2. Preserved specimen of *Rhytidopsis chelonites* from Col de la Pirogue, Mont Mou, New Caledonia showing pseudo-operculum. FMNH 144272. Collected January 23, 1962.

Figure 3. Preserved specimen of *Pararhytida dictyodes* from Col

de la Pirogue, Mont Mou, New Caledonia showing pseudo-operculum. FMNH 135440. Collected January 25, 1962.

Figure 4. Cross-section through tail of *Rhytidopsis chelonites* (FMNH 144272) showing pseudo-operculum (CP) and pedal grooves (FS).

numerous muscle fibers, which, in the main portion of the pseudo-operculum, have a predominately dorsoventral orientation. These muscles extend well beyond the pseudo-opercular pad into the tail proper, where the fibers run mainly in the longitudinal plane (Figure 5). It is clear from the preparations stained with Alcian blue that, unlike the usual exposed epidermis of pulmonates, the surface of the pseudo-operculum is devoid of mucocytes and other secretory cells.

When the animal retracts into the shell, the dorsal part of the tail angles across the plane of the aperture, with its posterior tip on the outer palatal wall and the anterior section against the parietal margin (Figure 1). The pseudo-operculum thus effectively fills the shell aperture. This functioning implies that the pattern of retraction of *Pararhytida* and *Rhytidopsis* into their shells is different from the pattern observed in most terrestrial pulmonate snails. In the latter, the tail itself is retracted until its posterior



Figure 5

Transverse section through tail of *Pararhytida dictyodes* from Mt. Canala, New Caledonia, 900–1050 m, New Caledonia. Collected January 21, 1979. Magnification 31.5 $\times$ .

tip lies above the pallial border. Space for this is provided by the lateral outward compaction of the lung cavity. Consequently only the mantle border is exposed in the plane of the aperture, and can thus secrete an epiphragm to separate the snail from the outside world. In both *Pararhytida* and *Rhytidopsis*, the tail remains distal to the pallial border, which may be related to the fact that the pseudo-operculum functionally replaces the epiphragm. Charopids and endodontids both secrete thin mucus sheets, and even taxa from drier Australian areas are not known to have calcareous thickening of the epiphragm (Solem, personal observations).

Although the exposed epithelial layer of the pseudo-operculum would be subject to evaporative water loss, presumably overall permeability would be reduced by the fibrous layer underneath. Instead of water passing freely from the entire tail surface to the exposed areas, it would have to flow around the edges of the pad, and, thus, less water would reach the evaporative surface itself. Contraction of the dorsoventral muscles in the pseudo-operculum could serve to expand the pad laterally and thus provide a better fit in the aperture. The exposed epithelial surface probably functions in respiration, since air flow to

the lung cavity would be severely impeded by the pseudo-operculum. It is also possible that the epidermis itself could actively reduce evaporative water loss, as has been shown in some European helicids (MACHIN, 1974; NEWELL & APPLETON, 1979).

The extent to which the pseudo-operculum gives actual protection against predation cannot be evaluated at present, but clearly the presence of a thick collagen fiber layer is potentially of great protective value. Rhytidids have been observed feeding on *Pararhytida* (Tillier, personal observations), but no analysis of rhytidid diets in New Caledonia has been attempted.

#### EVOLUTION OF THE PSEUDO-OPERCULUM

Geologically, New Caledonia is a fragment of the eastern border of Gondwana, which split off northeastern Australia during the Triassic, approximately 230 million years ago. It was possibly covered subsequently by two marine transgressions, but has been constantly exposed land since at least the Oligocene, or about 30 million years (PARIS & LILLE, 1977). As a result of this long isolation and existence as elevated land, the whole primary land snail fauna of New Caledonia is endemic at the specific level and many genera also are limited to New Caledonia.

The numerically dominant land snails of the family Charopidae show specializations in comparison with charopids elsewhere. The arboreal element is much better represented, and by far the largest species of Charopidae are found in New Caledonia.

A survey of body types in New Caledonian charopid land snails suggests a basic form dichotomy into (1) taxa with narrow, elongated tails that end in a prominent mucus pore and often a caudal horn, such as is common in the New Zealand otoconchine charopid genera (CLIMO, 1969:figs. 5A–F, 1971:figs. 1A–D) and (2) taxa with fairly short, often truncated tails, such as are found in typical Pacific Basin charopids (SOLEM, 1983:26, fig. 9a). The former tend to be arboreal in habits, the latter tend to be ground dwellers. Taxa of the *Rhytidopsis-Pararhytida* clade belong to the second morphological group, and are the only identified clade to be both arboreal and terrestrial.

The entire New Caledonian radiation of charopids is marked by a tendency towards large size, and *Pararhytida* includes the largest of all known charopids. Carnivorous land snails in New Caledonia reach moderately large size, *i.e.*, the 12–25 mm in diameter *Ptychorhytida* Möllendorff, 1903 and the 30–35 mm *Ouagapia raynali* (Gassies, 1863). These rhytidids are ground dwellers, and the large, litter-dwelling charopids would be logical prey for them. We do not know whether they feed exclusively on *Pararhytida*, but, as mentioned above, *Ouagapia* has been observed to feed on *Pararhytida*. The latter's habit of resting in the curled sheath portion of fallen palm fronds, not tightly sealed to the sheath surface, combined with the relatively large aperture of its shell, would leave the animals easy

victims for predatory ground snails. Any thickening of the exposed portion of the retracted animal that might discourage a feeding attempt would have selective value. Intensification of this trend would lead to the evolution of the pseudo-operculum. Because *Pararhytida* tends to be absent from the drier forests, we hypothesize that the pseudo-operculum functions primarily against predation.

Retardation of water loss would be a secondary benefit that might permit some members of the clade to utilize arboreal habitats, which are subject to greater humidity fluctuations, without any more morphological modification of the foot and lung cavity. The primacy of predation as a selective pressure in the evolution of the pseudo-operculum may find some confirmation from observations on the only terrestrial snails known to us that exhibit a pattern of animal retraction that is intermediate between the usual pattern and that found in the pseudo-operculate taxa. The large, African ground dwelling achatinids, for example *Achatina fulica* (Bowditch, 1822), when disturbed, do not retract their tail above the pallial border, but twist the tail so that its left side blocks the aperture, with the tip of the tail at the parieto-palatal margin (Binder, personal observation; also present authors). Subsequent full retraction and epiphragm building occurs in achatinids, so that this is not fully comparable, but this parallel behavior in an unrelated group is of interest. This use of the tail as a temporary and possibly protective block in achatinids suggests that possibly the primary adaptive value of the pseudo-operculum was protection.

A similar behavioral pattern involving exposure of the left side of the body after retraction into the shell has been noted in the fresh-water basommatophoran genus *Lymnaea* (STOREY, 1972, 1983). However, this pattern was observed only as a response to drought conditions, whereas simple withdrawal during short periods of inactivity left the sole of the foot exposed in the aperture. Storey was able to demonstrate a marked reduction in the rate of water loss from the exposed body wall when compared with the foot surface in retracted snails.

*Rhytidopsis* (diameter 6–8 mm) is much smaller than *Pararhytida* (diameter 14–37 mm). We assume that both are descended from an even smaller ancestor that was terrestrial in habitat. Evolution of the pseudo-operculum in the ancestor would have preceded both the arboreal shift by *Rhytidopsis* and the large size by *Pararhytida*. We view this evolution as a possible release mechanism for both changes.

Large size permits *Pararhytida* to fill the size gap for a herbivorous land snail between the typical small (2–4 mm) charopids and the huge New Caledonian *Placostylus* (some over 100 mm) of the family Bulimulidae. In other faunas, this size range is filled normally by members of the Camaenidae-Bradybaenidae-Helminthoglyptidae-Helicidae lineages. These taxa have much more complex kidney and ureteric structures (BOUILLON, 1960:fig. A) than are found in the Charopidae (Tillier, unpublished data). A normal

charopid, with its simple kidney and ureter, might not find wet enough niches in New Caledonia to reach large size. With the pseudo-operculum, and in the absence of competitive snail taxa, evolution of large size and exploitation of this size range became possible.

If these views are correct, it is clear that the pseudo-operculum that evolved under predator pressure has a selective value for size increase. In this sense, the pseudo-operculum is clearly an exaptation in the sense of GOULD & VRBA (1982:4): "features that now enhance fitness but were not built by natural selection for their current role."

The above speculations go well beyond available data, but it will be many years before systematic revisions of the New Caledonian land snail taxa are completed, permitting more accurate analysis of the ecological roles played by the constituent families. Adequate comparative data for the Australian, Melanesian, and New Zealand faunas also are lacking. But perhaps presentation of these ideas will help stimulate the work needed to test them.

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